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The relationship between productivity and tree-ring growth in boreal coniferous forests

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Ecosystem productivity estimated with a model calibrated with eddy-covariance data was related to tree-ring growth of two different boreal conifers along a latitudinal gradient. The relationship between ecosystem productivity and growth changed with species and site. Greater photosynthesis in spring and summer increased annual anomalies of radial growth in both species, and the response of growth to productivity was earlier in warmer southern stands particularly for pine. Radial growth of jack pine increased in the long-term with higher productivity, whereas this relationship was more reduced in black spruce. This could express species-specific differences in carbon allocation strategies but likely it is a consequence of the limiting marginal soils where spruce is found in the south. Only tree-rings of jack pine at some sites showed certain potential as direct proxies for ecosystem productivity at the low and high-frequency responses.

Introduction

Climate warming and the increase in atmospheric-CO_2 concentrations cause changes in forest growth and ecosystem productivity. There are reports of contrasting growth responses to warming over recent decades in different types of forests. Although some boreal species show negative growth trends in response to recent climate change (Hoofgaard *et al*. 1999, D'Arrigo *et al*. 2004), net ecosystem productivity in boreal and temperate conditions is generally expected to increase with increasing temperatures (Myneni *et al*. 1997, Boisvenue and Running 2006). Forest growth measurements and models assume that there is a close connection between the stem

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growth of a tree and its carbon balance (e.g. Running 1994, Le Roux *et al*. 2001, Zweifel *et al*. 2010). Variations in the net ecosystem productivity can be measured and modelled from networks of eddy-covariance towers (Kramer *et al*. 2002, Baldocchi *et al*. 2003, Bergeron *et al*. 2007) which provide useful insights into the carbon balances of ecosystems and their ecological drivers. However, since these towers are expensive to operate they provide limited temporal and spatial coverage of ecosystem carbon balances. Productivity estimates can also be derived from biometric-ecological inventory methods but these methods present similar shortcomings as those for eddy-covariance stations (Ehman *et al*. 2002, Gough *et al*. 2008, Ohtsuka *et al*. 2009).

Tree-ring records obtained using dendrochronological methods (Cook and Kairiukstis 1990) could be a key tool to extend carbon balances or ecosystem productivity to larger time scales and areas. Tree rings would be a useful complement to direct ecosystem productivity estimates since they extend both spatially and temporally beyond the directly measured data of net ecosystem exchange from flux towers. Additionally, a large quality checked archive of tree ring data is readily available from databases such as the International Tree-Ring Data Bank (ITRDB, http://www.ncdc.noaa.gov/paleo/treering.html). They have annual resolution and span many decades of forest growth. Traditionally, empirical models where climatic variables are regressed against tree growth indices were employed to fit the relationship between climate and growth in dendrochronology. Several authors developed mechanistic approaches of annual tree ring formation with more comprehensive process-based models that are also able to take into account the non-linear response of growth to climate (Foster & Leblanc 1993, Berninger *et al*. 2004, Misson 2004, Vaganov *et al*. 2006, Drew *et al*. 2010). These models try to mimic not only the influence of climatic factors, but can also account for phenology, radiation, changes in transpiration and other ecophysiological processes involving carbohydrate synthesis and allocation. The models perform well in explaining annual radial growth but generally not better than the classic, empirical approaches (Anchukaitis *et al*. 2006, Evans *et al*. 2006, Shi *et al*. 2008).

Several authors compared tree-ring growth with estimates of net primary productivity from mechanistic models (Rathgeber *et al*. 2003, Berninger *et al*. 2004, Girardin *et al*. 2008, Hari and Nöjd, 2009). Others studied the relationship between direct carbon flux estimates at eddy-covariance stations and tree-ring growth (Rocha *et al*. 2006), flux estimates and cambial growth (Zweifel *et al*. 2010) and flux estimates and biometric measurements of tree growth from permanent plots (Ehman *et al*. 2002, Gough *et al*. 2008, Granier *et al*. 2008, Ohtsuka *et al*. 2009). If ecosystem carbon fixation and ecosystem productivity could be estimated from tree rings, then dendrochronological data might provide an effective tool for the spatial and temporal extrapolation of micrometerological methods. However, to our knowledge no study has analyzed the variability in the relationship between growth and ecosystem productivity along a climatic gradient, since existing studies are concerned with local relationships between growth of stands around eddy-covariance stations and direct ecosystem flux measurements from the stations. Some agreement between ecosystem productivity and radial growth has been reported, yet these studies suggest that unknown carbon allocation strategies may obscure the growth–carbon relationship (Rocha *et al*. 2006, Gough *et al*. 2008, Ohtsuka *et al*. 2009). We analyzed the relationship between modeled ecosystem productivity and annual radial growth for two coniferous species sampled along a latitudinal (i.e. temperature and precipitation) gradient in eastern Canada. The growth data were originally published in Huang *et al*. (2010) who analyzed the relationship between the high-frequency of growth and climate using a classical empirical approach. Now we extend this work by using calculated ecosystem productivity as a covariate to investigate whether tree rings can be used as indirect estimates of ecosystem productivity. We split growth into its low- (i.e. to analyze the long-term multidecadal trends) and high-frequency (i.e. to analyze the short-term, annual response) components to analyze this relationship in the short and the long terms.

Material and methods

Tree-ring data: disentangling high- from low-frequency of growth

We analyzed the relationship between annual radial growth and net and gross ecosystem exchange in two boreal species from eastern Canada: black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). They are dominant post-fire species widely distributed in North America. Jack pine generally occurs at xeric sites with sandy soil, and black spruce generally occurs at sites with poor soil covered by thick moss layers (*see* Table 1 for further description on the sampled sites). In the south, black spruce stands mostly co-occur with balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*) and white pine (*Pinus strobus*). Jack-pine stands co-occur with black spruce and white birch (*Betula papyrifera*). In the north, monospecific pure stands of both species are frequently found. Samples were collected from dominant trees in dense, mature, un-managed post-fire stands.

Increment cores were collected from 20 trees from nine locations on a latitudinal transect from 46°N to 54°N (Table 1 and Fig. 1). Cores were processed and analyzed to build annual series of individual tree growth increments using standard dendrochronological methods (Cook and Kairiukstis 1990). Detrending methods in dendrochronology can emphasize either the long- or short-term growth response. We therefore split the analysis of the relationship between ecosystem productivity and growth in two: (1) a low-frequency analysis, using a variation of the regional curve standardization (RCS), which fits a single age-growth curve to all sites, and mixed models to study the response of growth to ecosystem productivity in the long-term; (2) a high-frequency analysis of the growth response to ecosystem productivity on each site separately to study how growth at the nine individual sites responded to productivity in the short-term (i.e. to annual growth anomalies). In both analyses, we used mean site chronologies of growth indices instead of individual tree growth series to pool out the influence of individual dendrometric features, thus making the growth indices comparable with estimates of ecosystem productivity.

Low-frequency analysis: I_{BAI}

For the low frequency analysis we used annual, basal area increments (BAI; *see* Fig. 2) with a

Table 1. Characteristics of sampling sites and sampled stands (black spruce and jack pine) along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest.

Species	Lat. (°N), long. (°W)	Elevation	Stand types (m a.s.l.)	Slopes(°)/aspect	Sample type
Black spruce	45°59′, 77°28′	183	Uneven-aged/Mixed	0	Cores
	47°03′, 79°20′	273	Uneven-aged/Mixed	0	Cores
	48°06′, 79°18′	260	Uneven-aged/Mixed	0	Cores
	49°09′, 78°32′	440	Uneven-aged/Mixed	2/N	Cores
	50°03′, 78°46′	260	Uneven-aged/Pure	4/S	Discs
	51°02′, 77°34′	240	Uneven-aged/Mixed	0	Discs
	51°52′, 77°26′	177	Uneven-aged/Mixed	0	Discs
	52°54′, 77°16′	226	Uneven-aged/Mixed	0	Discs
	53°39′, 78°22′	82	Uneven-aged/Mixed	5/E	Discs
Jack pine	46°00′, 77°25′	160	Uneven-aged/Pure	0	Cores
	47°02′, 79°21′	258	Uneven-aged/Mixed	0	Cores
	48°09′, 79°30′	330	Uneven-aged/Mixed	0	Cores
	49°09′, 78°32′	440	Uneven-aged/Mixed	7/N	Cores
	50°09′, 78°49′	245	Uneven-aged/Mixed	10/SE	Discs
	51°12′, 77°27′	215	Uneven-aged/Mixed	4/S	Discs
	51°56′, 77°22′	200	Uneven-aged/Mixed	0	Discs
	52°54′, 77°16′	226	Uneven-aged/Mixed	0	Discs
	53°42′, 78°04′	125	Uneven-aged/Mixed	3/N	Discs

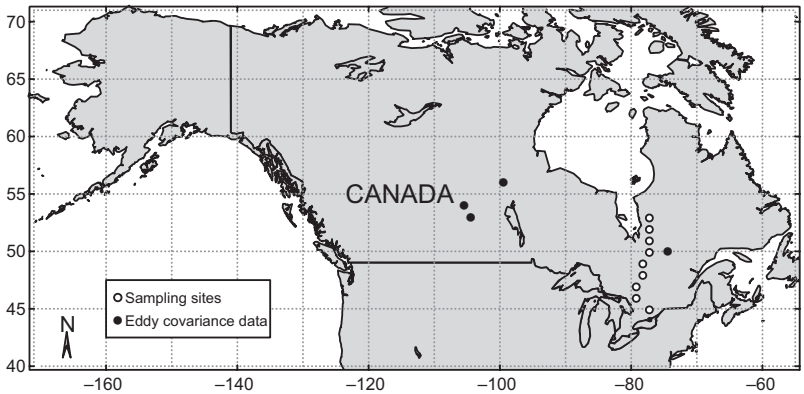

Fig. 1. Map of tree-ring sampling sites and eddy-covariance data utilized.

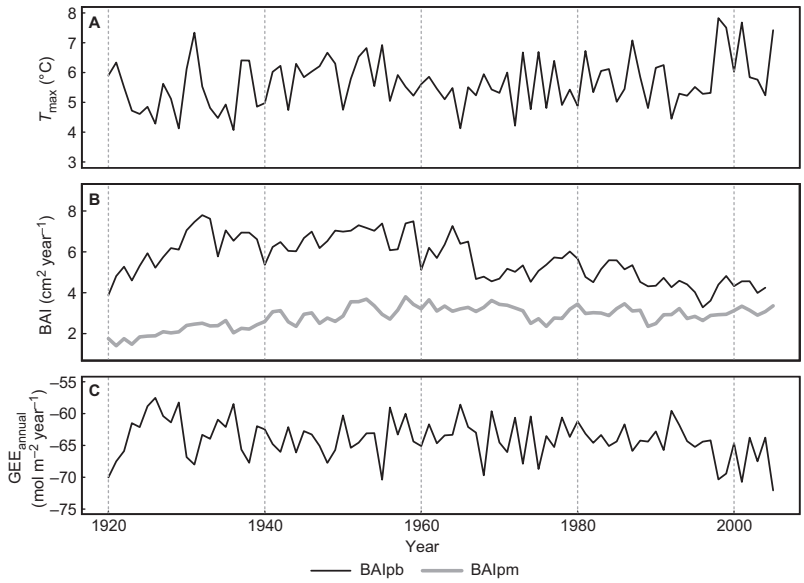

Fig. 2. Annual values and temporal trends of the calculated rates of photosynthesis (expressed as Gross Ecosystem Exchange, GEE), the Basal Area Increment (BAI) and the measured climatic variables. (**A**) Mean annual average maximum temperature averaged from the nine sites; (**B**) mean basal area increment (BAI) from *Pinus* (BAIpb) and *Picea* (BAIpm); (**C**) mean calculated annual GEE.

conservative detrending using the RCS method (Esper *et al*. 2003). Variance in BAI was first stabilized following Cook and Peters (1997) and then a mean single curve (Fig. 3) was fitted to cambial age aligned BAI series from all sites together to remove population average biological growth. We used a cubic spline with a 50% low-frequency cutoff of 150 years for jack pine and 250 years for black spruce (Fig. 3). These two values were selected to be close to the maximum age encountered in the sample from both species. Annual growth indices (I_{BAI}) were calculated using residuals between the fitted mean curve and observed individual BAI (Cook and Kairiukstis 1990). In the low-frequency analysis using I_{BAI}, we studied the relationship between growth and ecosystem productivity by analyzing the nine sites together so that we included a broader range in the covariates (calculated ecosystem productivity) to study the existence of non-linear relationships by fitting a single equation relating growth and climate.

High-frequency analysis: I_{RW}

In the previous, low-frequency analysis of the relationship between productivity and growth relationships we lose high-frequency site-wise information on the short-term relation of ecosystem productivity and tree growth. Therefore, to perform a parallel analysis with which we could study the site-wise short-term responses of growth we calculated a second set of growth indices after detrending individual ring-width (RW) series with 80-year splines (Cook and

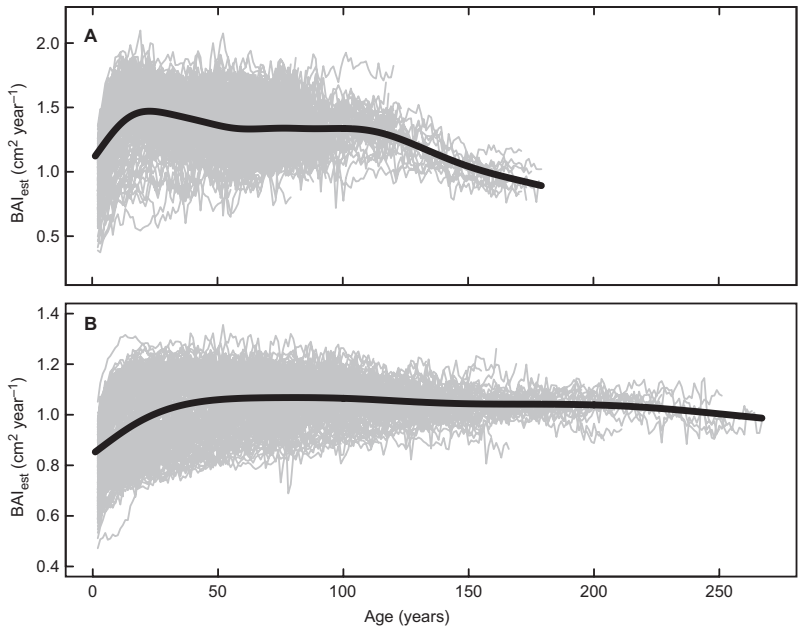

Fig. 3. Variance-stabilized Basal Area Increments (BAI_{est}) with spline fitted (150 and 250 years respectively for jack pine and black spruce) representing the average annual growth used to detrend data in I_{BAI}: (**A**) *Pinus banksiana* and (**B**) *Picea mariana.*

Kairiukstis 1990). Here, we analyzed the response of growth to ecosystem productivity at each of the nine sites separately.

Physiological covariates estimated from models calibrated with eddy-covariance data

We calculated time series of ecosystem productivity for each site using a photosynthesis model fed with local climate data obtained from Natural Resources Canada (Régnière and Saint-Amant 2008) for the nine sites studied. First, to calibrate the model we used integrated eddy-covariance gap-filled half-hourly carbon flux data coming from the four mature black spruce or jack pine forests included in the Fluxnet-Canada Research Network (http://fluxnet.ccrp.ec.gc.ca/e_about.htm) (Table 2 and Fig. 1). Daily flux data from the four forests were calculated from the half-hourly flux measurements and ecosystem carbon data were used to calibrate daily the model from Gea-Izquierdo *et al*. (2010, Appendix) based on Mäkelä *et al*. (1996, 2004). In this big-leaf model, stand gross ecosystem exchange (GEE, in mol CO_2 m^{-2} day^{-1}) was estimated as a function of atmospheric CO_2 concentration, photosynthetically active radiation, water vapor pressure deficit and air temperature. In the model, ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE) were calculated as NEE = R_{eco} – GEE. The model provided excellent fit to the four individual flux data sets (Efficiency, EF > 0.94 *see* Eq. 1 below for the meaning of EF) and also when fitted to the four sites together (EF = 0.97 for daily GEE and EF = 0.91 for daily respiration). Therefore, we fitted one single model to estimate carbon fluxes for all species and sites (Table 3 and Fig. 4; Gea-Izquierdo *et al*. 2010). Throughout the text, negative values of GEE and NEE correspond to a flux from the atmosphere to the land surface, i.e. GEE in all cases and NEE when photosynthesis exceeds respiration.

Once calibrated, the model was used to produce daily estimates of gross and net ecosystem productivity for the nine sites along the climatic gradient and these estimates were included as covariates in the low and high-frequency analyses. From the daily estimates calculated for the nine sites using the model, we obtained time series of monthly, seasonal and annual ecosystem productivity, to compare with growth indices. The following flux estimates (both year t and year t – 1) were evaluated in the I_{BAI} analyses: (i) annual GEE, NEE, and R_{eco}; (ii) spring GEE, NEE, R_{eco} (from April, May, June, which coincides with the annual maximum); (iii) growing

Table 2. Characteristics of eddy-covariance data sets used.

No.	Station in Canada	Lat. (°N), long. (°W)	Stand height (m)	Mean stand age	Altitude (m)	Dominant tree species	Period	NEE (mean ± SD) (μmol m^{-2} s^{-1})	Annual precip. (mm)	T_{mean} (°C)	Reference
1	NOBS	55.9, 98.5	10.6	150	259	*Picea mariana*	1994–2006	–0.534 ± 3.163	517.0	–2.9	Goulden *et al.* (1998)
2	Saskatchewan black spruce	54.0, 105.1	14	125	597	*Picea mariana*	1999–2005	–1.061 ± 3.409	405.6	0.8	Black *et al.* (2005)
3	Saskatchewan old jack pine	53.9, 104.7	14	94	520	*Pinus banksiana*	1999–2005	–0.677 ± 2.863	430.0	0.1	Howard *et al.* (2004)
4	Quebec old mature boreal forest	49.7, 74.3	20	120	382	*Picea mariana*	2003–2005	–0.627 ± 3.574	961.3	0.4	Bergeron *et al.* (2007)

season NEE, GEE and R_{eco} (April–September); (iv) the same for summer (June–August). The model estimates photosynthesis per ground unit area (m^2) of closed stands. We assumed that stand conditions (i.e. leaf area index and closed canopies) would remain unchanged along time and among sites. Later in the discussion we describe possible biases which could have arrived had we applied the same analysis to open stands or to stands with variable canopy conditions.

Statistical analyses

First, to analyze the differences between mean site responses (I_{BAI}, low-frequency) to physiological covariates we used linear mixed models including a random intercept for site (Verbeke and Mohlenberghs 2000). We studied the relationship between I_{BAI} as the dependent variable and physiological covariates on a single fit including all sites together. Serial correlation in the time series was taken into account by including a first auto-regressive, AR[1], variance-covariance error structure to each site submatrix. To compare models including GEE as covariate with those including GEE^2 (quadratic relationship) we used Akaike's Information Criterion (AIC) and the model minimizing AIC was considered to be the best (Burnham & Anderson 2004). Model performance was evaluated using the model efficiency (EF):

$$EF = 1 - \frac{(n-k-1)^{-1}\sum_{i=1}^{n}(y_i - \hat{\mu}_i)^2}{(n-1)^{-1}\sum_{i=1}^{n}(y_i - \bar{\mu})^2} \quad (1)$$

where n is the number of observations, k is the number of parameters, y_i is the ith value of measured variable y, $\hat{\mu}_i$ is the predicted value, and $\bar{\mu}$ is the mean of the measured variable). We used partitioning of variance to discuss the influence of each covariate (random and fixed) on the final model, which was calculated assuming that total variance equaled the sum of the individual variances of the different covariates within the linear models fitted. Secondly, for the high-frequency analysis, I_{RW} was compared separately for each of the nine sites with monthly estimates of the covariate explaining most vari-

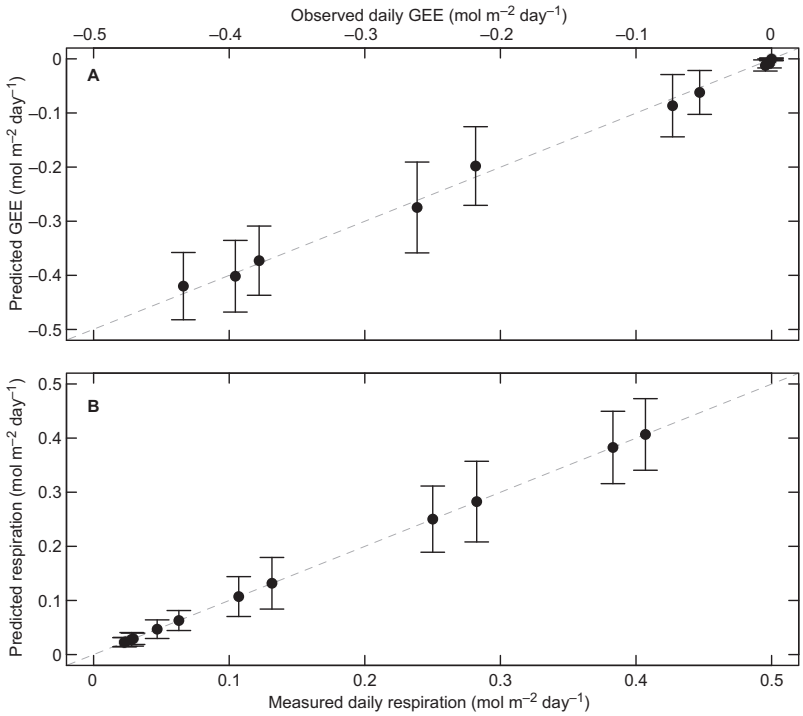

Fig. 4. Residuals of the fitted flux model expressed as monthly integrals of carbon flux: (**A**) GEE, (**B**) ecosystem respiration. Bars correspond to one standard deviation of the mean.

ance in the I_{BAI} analyses. To study the linear relationship between pair of variables we calculated Pearson's correlation coefficients (r_p) (Cook and Kairiukstis 1990).

Results

Long-term growth and productivity along the latitudinal gradient

NEE and GEE variables decreased with increasing latitude together with mean annual temperature and precipitation (Fig. 5; Huang *et al*. 2010). The mean BAI of both pine and spruce varied with age, in time along the 1900s and also at different sites (Figs. 2–4). There was a decrease of mean annual growth with latitude in pine (Spearman's correlation: $r_S = –0.867$, $p = 0.004$), but not in spruce (Spearman's correlation: $p = 0.291$; Fig. 5). The ecology and growth response to climate along the gradient differed between species, thus we analyzed the two species separately. Pearson's correlations between I_{BAI} and annual estimates of components of ecosystem productivity (i.e. NEE, R_{eco}, GEE) were slightly higher than those between I_{BAI} and summer or seasonal productivity, and correlations between I_{BAI} and seasonal and annual GEE and NEE were almost identical (Table 4). For this reason, hereafter we only report results using GEE covariates quoted as productivity.

High photosynthetic productivity enhanced tree growth (Table 5) and the relationship

Table 3. Best-fit model results for mean daily GEE model used to calculate ecosystem productivity series (Appendix). EF = efficiency (*see* Eq. 1 and definition in the text).

Observations	τ (days)	δ (μmol m^{-2} s^{-1})	α_{max} (mol m^{-2} day^{-1})	b	T_s (°C)	Bias	RMSE (mol m^{-2} day^{-1})	EF
10545	2.701	7.603	0.0016	–0.261	8.647	–0.001	0.032	0.967

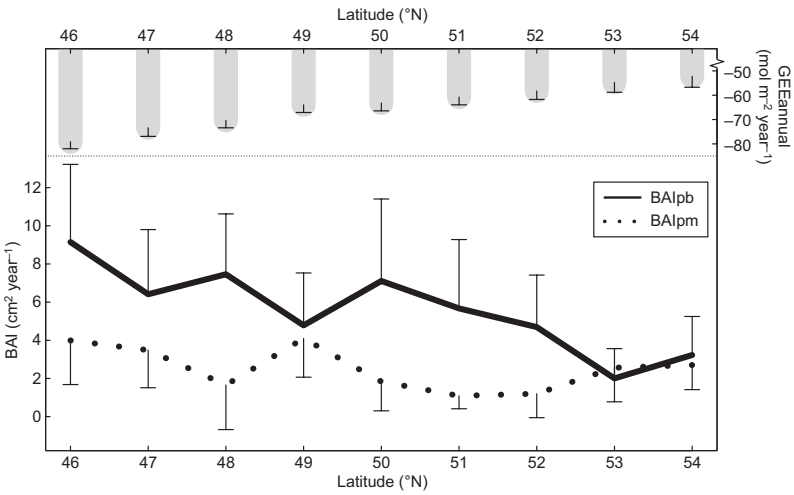

Fig. 5. Mean Basal Area Increment (BAI) of the two species analyzed and simulated mean annual GEE (grey bars, above) at the nine sites. Dashed black lines correspond to black spruce (BAIpm) whereas solid black lines to jack pine (BAIpb). Bars represent standard deviations.

between annual productivity and growth was quadratic for both species (AIC of the model as in Table 5 using GEE as covariate instead of GEE^2 was 11.7 units greater for pine and 13.5 units for spruce). However the contribution of random effects in the I_{BAI} model reflected mean differences in radial growth between sites and showed that in the low-frequency analysis the variability of annual growth explained by productivity was reduced for spruce (Fig. 6). The importance of random effects was much greater in the spruce model, where the fixed effects were explaining a very small part of the total variance (Table 5 and Fig. 6). As seen in Table 6 the performance of the I_{BAI} model had not been good if analyzed site-wise because this analysis neglected the high-frequency local responses to ecosystem productivity, which we analyze below.

Table 4. Pearson's correlations (r_P) between growth index from the low-frequency analyses (I_{BAI}) and CO_2 fluxes (GEE, NEE, R_{eco}) for *Pinus* and *Picea*.

	GEE_{annual}	$GEE_{anual(t-1)}$	GEE_{season}	GEE_{spring}	GEE_{summer}	NEE_{annual}	R_{eco_annual}
I_{BAI} *Pinus*	–0.626	–0.614	–0.623	–0.583	–0.623	–0.625	0.624
I_{BAI} *Picea*	–0.275	–0.263	–0.250	–0.255	–0.265	–0.274	0.264

Table 5. Model results: the model for site i is: $I_{BAIi} = (\mu + a_i) + \beta GEE^2 + \varepsilon_i$, with a_i being a random site effect, ε_i the random error; μ a common intercept for the whole population and β a fixed coefficient for GEE^2 (the quadratic function of GEE). GEE = annual GEE; EF = efficiency calculated including the fixed and random site effects (Eq. 1); SE = standard error; AR[1] = parameter estimate of first order autoregression used in the variance-covariance structure for the error.

GEE model		Parameter (covariate)	Estimate	SE	EF
Pinus banksiana	Fixed effect estimates	μ	–0.0599	0.0325	49.18
		β (GEE^2)	5.61×10^{-07}	1.01×10^{-10}	
	Covariance estimates	Random intercept (site)	0.0058	0.0041	
		AR[1]	0.8931	0.0023	
Picea mariana	Fixed effect estimates	μ	0.03113	0.0171	50.08
		β (GEE^2)	6.14×10^{-8}	1.00×10^{-10}	
	Covariance estimates	Random intercept (site)	0.0018	0.0013	
		AR[1]	0.9377	0.0163	

Local responses to short-term variations in productivity

Results from the high (I_{RW}) frequency analysis were different from those of the low-frequency (I_{BAI}) analysis (Fig. 7). Differences between species in correlation values between monthly-simulated productivity and I_{RW} were smaller than those in the low-frequency I_{BAI} analyses (Fig. 7). Yet linear correlation coefficients between covariates and I_{RW} for pine were still generally greater than those for spruce (Fig. 7). In pine, growth of stands located more to the south (latitudes 46°–50°) responded to photosynthesis earlier in spring (particularly at year *t*) while trees from northern stands responded later in summer (Fig. 7A). The positive response of growth to productivity in black spruce was more homogeneous along the gradient in spring, and the delay in the response with latitude was less evident, particularly in the current year (Fig. 7B). Growth of spruce at low latitudes exhibited a stronger negative response to high productivity in summer of the current year. In contrast, the effect of high productivity in the summer was positive for growth at the highest latitudes for the same period. These effects in summer were detectable for both species also for the previous year. In pine there was a strong relationship between growth and productivity of the previous year, with some differences between latitudes.

Discussion

Process-based growth models generally contain sets of equations of photosynthetic production and respiration, as well as rules of how this photosynthetic production is allocated to different plant organs. In the present paper, we estimated tree-ring width at different temporal scales as a direct function of photosynthetic production. The proposed approach is a modification to that in Berninger *et al*. (2004) who presented relationships between leaf-level photosynthesis and growth of Scots pine and similar to that in Foster and Leblanc (1993) or Federer *et al*. (1989). Detailed ecophysiological growth models require knowledge of stand structure and its changes over time (Berninger *et al*. 2004).

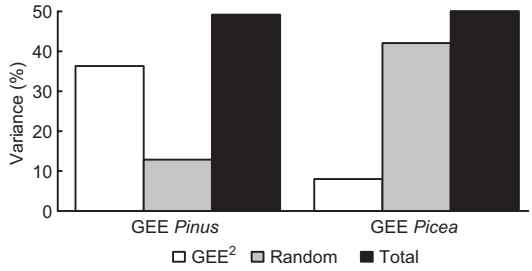

Fig. 6. Partition of variability contribution (%) of fixed effects and random effects for the GEE jack pine model ('GEE *Pinus*' in the *x*-axis) and GEE spruce model ('GEE *Picea*' in the *x*-axis) expressed as percentages of efficiencies (EF) of those covariates and total efficiencies shown in Table 5.

This information is, however, rarely available. Permanent sample plots are usually measured only every five years or even less frequently and reconstruction of tree growth with a high temporal resolution depends largely on tree rings. Photosynthetic production depends on the climate and properties of the plant canopy (e.g. Le Roux *et al*. 2001). The present modeling approach keeps the canopy characteristics fixed and focuses on the estimation of the climatic effects on photosynthesis as e.g. in Mäkelä *et al*. (2008a) or Gea-Izquierdo *et al*. (2010). We acknowledge that there are changes in forest productivity associated with changes in the physiological properties of leaves (Kaufmann *et al*. 2004) and forests in more productive areas or during more productive periods would probably have higher leaf area index (LAI), hence higher photosynthetic production. However, we

Table 6. Contribution of individual fixed effect (GEE^2) to the explained variability for *Pinus banksiana* and *Picea mariana* if calculated by site using the overall I_{BAI} models in Table 5. All values are percentages.

Site	*Pinus banksiana*	*Picea mariana*
46°	0.05	0.56
47°	0.04	2.08
48°	0.47	0.68
49°	1.36	2.48
50°	0.08	0.38
51°	0.05	0.31
52°	1.01	1.86
53°	7.14	0.44
54°	1.72	1.37
Mean (SD)	1.32 (2.27)	1.13 (0.83)

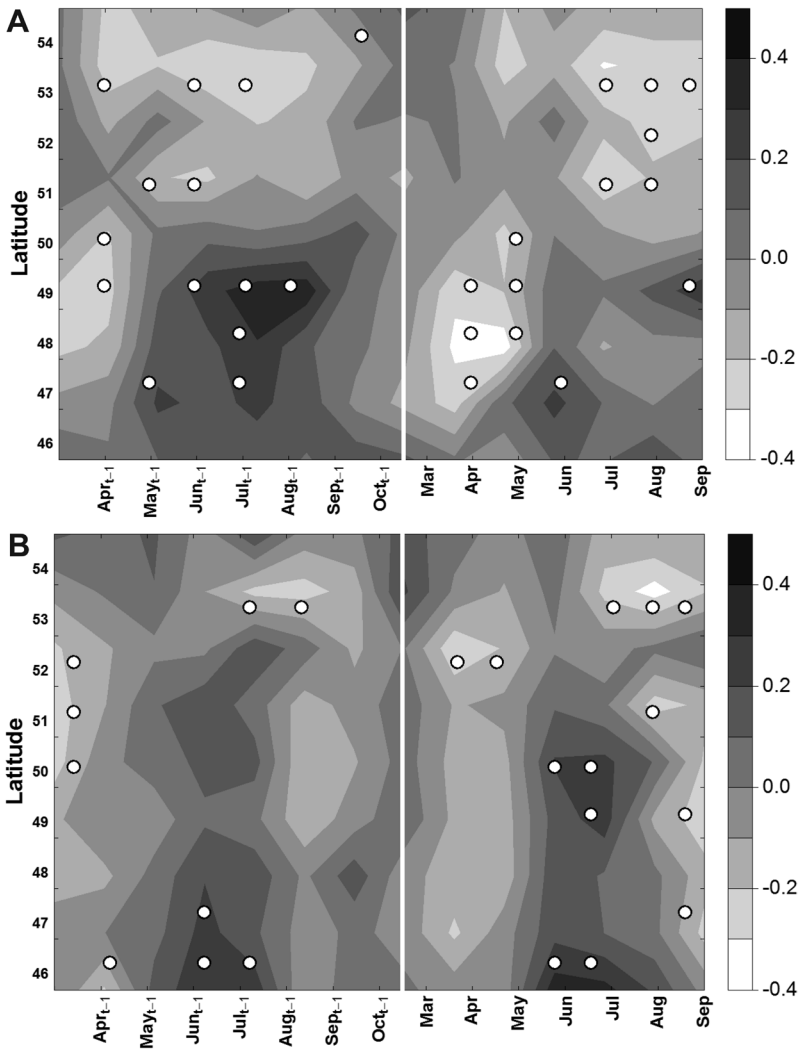

Fig. 7. Bootstrap correlations between individually detrended RW (I_{RW}) data and monthly GEE (from April to November year $t-1$, and from March to September year t): (**A**) *Pinus banksiana* GEE, (**B**) *Picea mariana* GEE. White dots indicate significant correlations. Note that high negative GEE values indicate the forest being a carbon sink hence negative correlations between growth and GEE express that greater photosynthesis at a specific period increases growth. The grey scale represents Pearson's correlations ranging between –0.4 and 0.5.

do not think that this would change qualitatively our results because annual fluctuations of tree growth are directly linked to lagged GEE (i.e. through and autoregressive model). Hence similar relationships between photosynthetic production and tree ring width would be maintained, particularly when studying growth anomalies in the high-frequency analysis.

Time-scale, species-specific relationships between radial growth and productivity

The relationship between ecosystem productivity and radial growth is complex. Tree-ring growth reflected both long- and short-term variations in site productivity but not equally for all sites and species. The long-term mean gross ecosystem exchange was well related only to annual radial growth of one boreal evergreen coniferous species along a latitudinal gradient, jack pine, whereas the correlation with black spruce was very weak. In the short-term, annual anomalies of tree growth were well related to simulated productivity at all sites and for both species. The fit of this relationship (absolute maximum correlation values around 0.4; Fig. 7) was similar to that found for empirical dendroecological models using temperature or growing degree days as the

main driver (Hofgaard *et al*. 1999; Huang *et al*. 2010). Results from tree-ring empirical models are often similar to results from process-based approaches (e.g. Berninger *et al*. 2004, Anchukaitis *et al*. 2006, Evans *et al*. 2006, Shi *et al*. 2008). The reason for the similar performance of photosynthesis based and climate based empirical models could be that the non-linear relationship between temperature (in our boreal stands) and photosynthetic production converged to linear when analyzed in long time periods.

The differences in the time scale of the relationship between growth and productivity could explain why models of ecosystem productivity and tree growth seem to operate on different processes. Ecosystem productivity in boreal forests where drought is usually not limiting seems to depend largely on the length of the photosynthetically active period (Suni *et al*. 2003a, 2003b) which usually starts in April or May. Annual tree diameter growth anomalies, on the other hand, seem to depend on summer temperatures (Kirdyanov *et al*. 2003, D'Arrigo *et al*. 2004, Vaganov *et al*. 2006) and growth can correlate quite well with temperatures during short periods (Kirdyanov *et al*. 2003). Cambial activity is temperature-dependent and varies at different sites and for different species, but higher temperatures are required for xylem cell division than for photosynthesis in the leaves (Körner 1998, Suni *et al*. 2003b, Rossi *et al*. 2011). Therefore, time-scale dependent relationships exist between net carbon fixation and growth and the relationship between these two variables is not a fixed ratio (Luyssaert *et al*. 2007, Granier *et al*. 2008, Zweifel *et al*. 2010). Trees in boreal forests are considered to use the period of maximum productivity to allocate carbon to the stem for growth, and this period is delayed in summer with increasing latitude (Kirdyanov *et al*. 2003). After summer, during those months prior to the dormant period, the trees store carbohydrates for next year's growth (Granier *et al*. 2008) and year-to-year variations in productivity could be averaged out by changes in carbohydrates reserve or allocation, which results in more diffuse and difficult to detect relationships between GEE and growth.

Our results agree with those of authors showing a correlation between the high-frequency of growth and photosynthesis (Berninger *et al*. 2004, Hari and Nöjd, 2009, Zweifel *et al*. 2010), but different relationships were found for the different sites. Allocation of carbohydrates was the most likely mechanism explaining differences in the growth response between sites and species. Rocha *et al*. (2006) explained the lack of correlation between measured GEE and ring width on a black spruce site in northern Canada by interannual differences in allocation. Granier *et al*. (2008) suggested that carbon allocation from photosynthesis is constant during the period when cambium is active in *Fagus sylvatica* but carbohydrate allocation is a complex phenomenon that is likely to vary with species and also other factors such as climate, soil or even competition (Gough *et al*. 2002, Rocha *et al*. 2006). Furthermore, there is evidence for systematic changes in allocation with varying temperature and an interaction of precipitation with temperature along climatic gradients (Vogel *et al*. 2008). In practice this means that the short-term tree growth may be decoupled from photosynthesis and that trees may modify their growth in response to long-term changes in photosynthetic production (D'Arrigo *et al*. 2004, Kaufmann *et al*. 2004). Zweifel *et al*. (2010) showed the potential complexity of the relationship between growth and photosynthesis and found a strong correlation between cambial activity and GEE which was a function of the time scale, as was also found by Granier *et al*. (2008). Stronger correlations can be expected at single sites where both flux and growth are measured (e.g. Zweifel *et al*. 2010) as compared with cases where productivity needs to be simulated along climatic gradients, like we did here.

Other factors precluding a general direct relationship between growth and productivity

Stand-related factors such as stand density, characteristics of tree individuals or microenvironmental variability could also modify the relationship between photosynthesis and growth. To minimize the influence of competition and tree dendrometric features at the different sites we selected mature stands with closed canopies, similar to those used to calibrate the photosynthesis model. However, selection of only

dominant trees, as done classically in many dendrochronological studies, may bias estimated stand growth and its relationship with stand photosynthesis. We believe that the influence of this was minimal at the sampled sites because stands were post-fire, closed and structurally homogeneous. The differences among sites and between species in our results could also be explained by non-climatic factors such as nitrogen availability (Mäkelä *et al*. 2008b), insect infestation in spruce (Bouchard *et al*. 2005), different litter decomposition and nitrogen mineralization rates (Bergh *et al*. 1999, Berninger *et al*. 2004) or the effect of the humus layer on a differential response to drought (Drobyshev *et al*. 2010). Only jack pine decreased its mean radial growth with increasing latitude, hence site temperature and productivity, indicating that climate controlled most of what foresters call 'site quality' for jack pine. For spruce, differences between sites in average growth seemed to be determined by non-climatic factors. Black spruce occupies many different environments in the boreal region of North America, but is not very competitive on eutrophic sites. Those sites occupied by black spruce change along the gradient studied: in the North it is a generalist growing on all types of sites (including good sites), whereas in the south it is restricted to poor sites (Burns and Honkala 1990, Hofgaard *et al*. 1999). This shift of the realized niche of black spruce could explain its low response to changes in average simulated GEE along the gradient.

NEE was not better correlated with radial growth than GEE probably due to the fact that the fraction of autotrophic to heterotrophic respiration was highly variable between sites (Lloyd and Taylor 1994, Xu *et al*. 2004). Estimated respiration was closely related to NEE and GEE estimates, but its correlation with growth was weaker than with GEE, contrary to Rocha *et al*. (2006) but in accordance with Zweifel *et al*. (2010). However, according to the literature, respiration is only a minor component of interannual variability in carbon fluxes in boreal forests (Suni *et al*. 2003a, 2003b) while respiration seems to be a major determinant of inter-site variability of net productivity (Valentini *et al*. 2000, Luyssaert *et al*. 2007). It could be that a varying proportion of GEE is fixed by vegetation in the understory (Knorre *et al*. 2006). It could be argued that our GEE model was not applicable given the distance between our sites and three of the flux towers used for the model calibration. The southern stands were in more temperate climate than the eddy-covariance sites, and we found a different response to GEE in summer (particularly of the previous year) for southern sites as compared with that for sites located more to the north. Therefore, it is possible that the photosynthetic production at these sites was more limited by drought than in our calibration data set, and that we overestimated photosynthetic production during summer in the southernmost stands. This would explain the inverse relationship between summer photosynthetic production and growth (expressed as a positive relationship in Fig. 7) for southern sites. Nevertheless in the eddy-covariance-based analysis of Gea-Izquierdo *et al*. (2010) drought did not appear to affect the estimated GEE at any site with mean temperature below 2.5 °C, like those included in our gradient (Huang *et al*. 2010). In that paper, the authors tried to incorporate the effects of drought into the model, but concluded that the effect of drought was minor. Additionally the model had a good fit to coniferous GEE data regardless of species or geographical locations, and the same type of model with small changes in parameters could be used for different sites along a climatic gradient including sites below 46°N (Gea-Izquierdo *et al*. 2010). The reason for the better fit for jack pine was not in the photosynthesis model since the photosynthesis model was calibrated using mostly black-spruce stands. We therefore believe that using a single GEE model on the geographical gradient studied did not lead to biased results that would compromise our conclusions.

In boreal ecosystems, temperature is generally the strongest driver of photosynthesis and growth and recent decades warming mostly resulted on an increase in photosynthetic activity (Myneni *et al*. 1997), as reflected by our productivity estimates. Pine growth showed a time trend that we interpreted as an age effect but could also be interpreted as a growth decline reflecting a drought effect in recent years (e.g. Hofgaard *et al*. 1999, Dulamsuren *et al*. 2010). However, trees older than 120 years were only found at

53°N (the second northernmost site) and our high-frequency analysis suggests greater water limitations in spruce than in pine. We would expect (if any) water stress limitation to be more widespread in southern stands (Hofgaard *et al*. 1999) and in any case, any existing age trend did not affect our analysis because growth data were standardized using dendrochronological methods. We analyzed high-frequency and low-frequency responses separately in our paper. The high-frequency is likely to be of secondary importance in long-term growth trends under climate warming and also in terms of productivity. We still do not understand how long-term changes in net productivity and photosynthesis allocation to stem growth will interact. Growth changes in the future may be, therefore, different than just changes in photosynthetic production.

Conclusions

The relationships between estimated ecosystem productivity and tree-ring width were different for the two species depending on the temporal scale analyzed and along the studied climatic gradient, probably reflecting differences in phenology and species-specific carbon allocation strategies. The year-to-year response of growth (annual anomalies from the site mean) was enhanced by ecosystem productivity in both species whereas the long-term relationship of average tree annual growth with ecosystem productivity showed a good agreement with overall photosynthesis only for jack pine. Probably long-term variations in net photosynthesis change the response of growth to climate, which also depends on non-climatic factors. There is a considerable potential to understand these variations and use tree-ring growth as a proxy for ecosystem productivity but this would require a deeper understanding of the possibly interfering factors, in particular of interannual variations in carbohydrate allocation.

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Appendix

NEE was modeled using a flux partitioning algorithm where: NEE = R_{eco} – GEE, with GEE being gross ecosystem exchange (photosynthesic production) and R_{eco} being ecosystem respiration. All C flux estimates are in mol m^{-2} day^{-1}. R_{eco} was modeled assuming an Arrhenius type relationship with air temperature, using the expression:

$$R_{eco}(t) = R_{10} \exp\left\{308.56\left[\frac{1}{56.02} - \left(\frac{1}{\left[T_{air}(t) + 46.02\right]}\right)\right]\right\} \quad \text{(A1)}$$

where $T_{air}(t)$ is the measured temperature (°C) above the canopy and R_{10} is the mean respiration at 10 °C. After comparing different ways of temporal fitting (monthly, every second week, annual), we decided to fit a single expression per site since the differences in the proportion of explained variance were not very large.

In the model, the gross photosynthetic rate per unit ground area $A(t)$ (mol CO_2 m^{-2} day^{-1}) was modeled as a nonlinear function of stomatal conductance of carbon dioxide $g(t)$ (mol CO_2 m^{-2} day^{-1}), photosynthetic capacity $\alpha(t)$ (mol CO_2 m^{-2} day^{-1}), and a saturation function of light intensity $\gamma(t)$ (dimensionless):

$$A(t) = \frac{g(t)C_a\alpha(t)\gamma(t)}{g(t)+\alpha(t)\gamma(t)} \tag{A2}$$

where the stomatal conductance is expressed as:

$$g(t) = \max\{0.00001, \tilde{g}(t)\}, \tag{A3}$$

with

$$\tilde{g}(t) = \left(\sqrt{\frac{C_a 10^{-6}\lambda}{1.6D(t)}} - 1\right)\alpha(t)\gamma(t) \tag{A4}$$

and the light response of biochemical reactions of photosynthesis:

$$\gamma(t) = \frac{Q(t)}{Q(t)+\delta} \tag{A5}$$

where C_a is the air CO_2 concentration in ppm, $Q(t)$ is the incident photosynthetically active radiation (μmol m^{-2} s^{-1}), $D(t)$ is the water vapor pressure deficit (kPa) calculated using temperatures above the tree canopies, δ is the half saturation parameter of the light function (μmol m^{-2} s^{-1}) and λ is a model parameter expressing the carbon required in the long term to sustain transpiration flow (kPa). λ was set to 3000 as in Gea-Izquierdo *et al*. (2010).

Photosynthetic capacity $\alpha(t)$ was modeled as a lagged function of temperature $S(t)$, following:
with

$$\alpha(t) = \alpha_{max}/\{1 + \exp[b(S(t) - T_s)]\} \tag{A6}$$

and, $S(t)$ from

$$\frac{dS(t)}{dt} = \frac{T_{air}(t) - S(t)}{\tau} \tag{A7}$$

$T_{air}(t)$ is the measured air temperature (°C) at time t, and α_{max} (mol m^{-2} day^{-1}), b ($°C^{-1}$), T_s (°C) and τ (days) are the model parameters: α_{max} is the maximum photosynthetic efficiency, which takes into account whole canopy properties; b is the curvature of the sigmoid function and T_s is the inflection point of the sigmoid curve, i.e. the temperature at which α reaches half of α_{max}; and τ is the time constant of photosynthetic acclimation and indicates the time it takes for photosynthetic capacity to acclimate itself to changing temperature. All original references to the different parts of the model and a further explanation on the model can be found in Gea-Izquierdo *et al*. (2010).